Polarity and regeneration in plants

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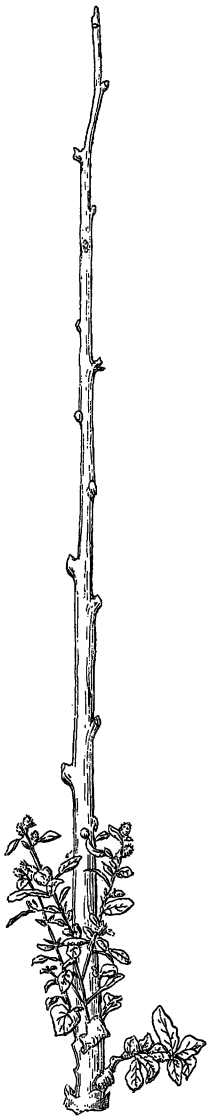
The earlier and greater development of the buds that stand at the distal end of a piece of a willow than of those that stand nearer to the base of the piece bears a certain general resemblance to the phenomenon of polarity in animals, and has led, in fact, to the use of the same word for both processes. This comparison needs, I think, to be more critically examined. During the past summer I have kept pieces of several plants, from which the leaves were removed, in a moist chamber with the lower end of the pieces in water, and have watched the development of the buds. In most cases, as in the willow, the more distal, *though not necessarily the most distal*, buds are the first to develop, and it could be easily seen that those that unfolded first were, as a rule, the largest and most advanced buds present on the piece when it was removed from the plant. In other words, the relative strength of the buds determines which develop first, and it seems most plausible that in consequence of this development the other buds might be kept from unfolding because those that got the start used up all the available food substances that were present, or were being manufactured in the piece. It appears, therefore, that the result is not so much the outcome of the polarity of the piece, acting at the time of regeneration, as of preexisting conditions in the piece at the time of its removal from the plant. These determine which buds shall be the first to unfold. Whether or not this difference in the condition of the buds of the original piece has itself been regulated by polar relations in the growing point is a question for further consideration, but in any case it is one that does not involve the immediate question of the regeneration of the isolated piece.

In one of the plants that I examined, the proximal and not the distal buds of the piece were the first to develop. It is this case that I wish more especially to discuss in connection with the problem of polarity in plants. The plant was the common burdock, *Arctium Lappa* (*Lappa officinalis*). The leaves and the lateral branches were cut off from half a dozen vigorous plants, and the

denuded stalk was left standing in place in connection with its original roots. In the course of about ten days new buds began to grow out near the base of the stalk. They unfolded rapidly and at the end of about two weeks had reached the condition shown in the figure. The new shoots arose in or near the angles between the main stem and the lateral branches (which had been cut off). These branches stand in the axils of the lower leaves. No shoots at all appeared in the upper regions of the stem, although the latter remained green and in good condition. It may appear that the results in this case are connected with the attachment of the stem to the old roots. The fact that large branches arise near the base of the main stem may be interpreted to mean that these parts receive a large share of the substances that come up from the roots. In order to see if this suggestion had any value I cut off other stems from their roots, stripped them of their leaves and branches, and placed the lower ends in dishes of water. In these cases also the lower buds alone unfolded and none appeared in the upper parts of the stem.



To determine whether the result is due to the better development of the buds at the base rather than due to the movement towards the base of food or of so-called formative substances, I cut a few of the stems into three pieces. In those in which any development took place this occurred in the basal pieces, and in one case in the lower part of the second piece as well, but no buds developed in the distal pieces, although to all appearances these remained in good condition. Whether these distal pieces would after a much longer time (I kept them nearly three weeks) have developed buds, I do not know.

This last experiment, while not satisfactory in all respects, yet suffices to show that the development of the basal buds in the long pieces is not due to the polarity localizing, as it were, the development at the base, nor to the flow of substances downward, but is due to the stronger buds being present in the basal region.

These results recall the cases of *Lilium candidum* and *Lachenalia luteola*. These plants do not set seed, but produce bulblets at the base. This formation of basal bulblets is attributed by Goebel to the flow of food substances in the plants towards the base which causes the bulblets to develop in this region, and at the same time deprives the seeds of the necessary material for their development. The explanation appears to me to be exactly the reverse. The buds that give rise to the bulblets in these plants are so vigorous that they utilize all of the food substances that are present, and thus deprive the seeds of food material that they might possibly make use of if the bulbs did not develop. It is not, I think, the flow of food substances downwards that causes the bulblets at the base to develop, but the vigorous bulblets in this region draw into themselves so much of the available food substances that not enough is left for the seeds.

It might be claimed in the case of the burdock, that when the stalk, deprived of its leaves, is left attached to the old roots, material from the roots rising up into the stem will affect the basal buds first; or it might be claimed that since there are large fibro-vascular bundles that go to the basal nodes these bring to this region materials from the roots that cause the buds to develop, but that this is not the real explanation was shown above by the experiment of removing the stem from the roots. The result appears to be due rather to the more vigorous condition of the basal buds. Whether, as I have said, this condition of the plant is itself to be thought of as ultimately the outcome of its polarity, is a question that I do not think we can profitably discuss as yet. If it is, then the polarity in the growing point has already acted and determined the relative development of the buds in the different regions. When the piece containing these buds is removed, their further development is first determined by the stage that they are already in, or by their greater vigor, which may, in most cases, mean the same thing. In the second place certain buds having gotten a start use up all or most of the available food materials and thus check the further development of the other buds.

In the light of these facts and conclusions certain of the statements that I made in my book on "Regeneration" in regard to the cause of the development of the apical buds in a piece of the willow must be recast. The development of the apical buds of the willow, and of other similar plants, and of the basal buds in the burdock appear both to be due, not to a dynamic relation (polarity) between the two ends of the piece, but to a static condition already existing in the piece before its removal, namely, the relative state of development of its buds.

From this point of view Sachs' theory of formative stuffs plays no directive part in the regeneration of pieces of the plants. The presence of food stuffs enters into the problem only in so far as certain parts are supposed to be able to draw on that which is present, while other parts (the less developed buds) are not so able to make use of the common supply. The flow of these food stuffs through the plant appears from this point of view not to be due to the stuffs tending to flow of themselves in certain directions, or as the result of the action of some outside agent, as gravity, but their flow may be simply a question of diffusion from those places where they exist in larger amounts to other places where there is not so much of the substance present. If the more vigorous and somewhat older parts can make use of this material more rapidly than can the less well-developed parts, there will be a steady flow of soluble food substances towards the growing parts, because in these regions the material is being more rapidly used up, and hence the region is relatively poorer in these materials. The flow is then a purely physical problem. This assumption is, of course, not different from that usually employed by botanists to account for the flow of soluble substances from one part of a plant to other parts.

It appears, therefore, that polarity in the plant is not the cause of the flow of substances through the plant, as Goebel seems to imply in certain parts of a recent article,* nor does polarity appear to regulate the development of certain buds and hold others in check.† Possibly some such factor may determine in the growing regions of the plant the relative rate of development of certain buds, but even this is not certain and remains to be further examined.

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* Goebel. Bull. Torrey Club, 30: 197–205. 1903. Also Biolog. Centralbl. 22: 385–397, 417–438, 481–505. 1902.

† Morgan. Bull. Torrey Club, 30: 206–213. 1903.